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Age, year-class strength variability, and partial age validation of *Coregonus kiyi* from Lake Superior

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Abstract

Age estimates of Lake Superior Kiyi *Coregonus kiyi* from scales and otoliths were compared and 12 years (2003-2014) of Kiyi length frequency data were examined to assess year-class strength and validate age estimates. Ages estimated from otoliths were precise and were consistently older than ages estimated from scales. Maximum otolith-derived ages were 20 for females and 12 for males. Age estimates showed high numbers of fish aged 5, 6, and 11 in 2014, which correspond to the 2009, 2008, and 2003 year-classes, respectively. Strong 2003 and 2009 year-classes, along with the 2005 year-class, were also evident by distinct modes of age-1 fish (<110 mm) in the length frequency distributions from 2004, 2010, and 2006, respectively. Modes from these year-classes were present as progressively larger fish in subsequent years. Few to no age-1 fish (<110 mm) were present in all other years. Ages estimated from otoliths were generally within one year of ages corresponding to strong year-classes, at least for fish age-5 and older, suggesting that Kiyi age may be reliably estimated to within one year by careful examination of thin-sectioned otoliths.

<A>Introduction

Kiyi *Coregonus kiyi* is one of eight cisco species (*C. alpenae*, *C. artedi*, *C. hoyi*, *C. johannae*, *C. nigripinnis*, *C. reighardi*, and *C. zenithicus*) that historically existed in the Laurentian Great Lakes (Koelz 1929). Kiyi were found in Lakes Huron, Michigan, Ontario, and Superior (Koelz 1929), but presently occur only in Lake Superior (Eshenroder et al. 2016). The demise of Kiyi in the other Great Lakes is not well understood, but may have been due to increased abundances of Alewife *Alosa pseudoharengus* and Rainbow Smelt *Osmerus mordax* (Christie 1974), overfishing (Moffet 1957; Smith 1964; Parker 1989), or introgression to a generic deepwater cisco swarm by interbreeding with other deepwater cisco species (Eshenroder et al. 2016). In contrast to Lakes Michigan and Huron, Kiyi in Lake Superior appear to have retained their morphological characters and have not introgressed to a species swarm (Eshenroder et al. 2016). Kiyi is presently the most abundant deepwater (>100 m) pelagic species in Lake Superior (Yule et al. 2013).

Accurate age estimates are fundamental to understanding the life history and population dynamics of fish (Beamish and McFarlane 1983). However, age estimation can be difficult for long-lived fishes because of crowded annuli on the margins of calcified structures due to slow growth (Campana 2001). Systematic underestimation of fish age can lead to overestimates of growth and mortality rates (Mills and Beamish 1980) and compromise understanding of year-class strength (Yule et al. 2008). Maximum reported ages of Kiyi in earlier studies using scales were 6 years from Lake Ontario (Pritchard 1931) and 10 years from Lake Michigan (Deason and Hile 1947). More recent otolith-based maximum age estimates for Lake Superior Kiyi were >20 years (Gorman 2012; Pratt and Chong 2012). These results agree with others who found that age estimates derived from otoliths and fin spines or rays typically exceed age estimates derived from scales (Maceina et al. 2007; Quist et al. 2012). A comparison of scale and otolith-derived ages of Kiyi has not been conducted, nor have the ages of deepwater ciscoes been validated, *sensu* Beamish and McFarlane (1983).

High interannual variation in year-class strength was not historically described for Laurentian Great Lakes cisco species (Koelz 1929). Dryer and Beil (1964) observed a minor 2 to 3-fold fluctuation in year-class strength in Lake Superior Cisco *C. artedi* based on commercial fishery landings from 1950-59 and scale-derived age estimates. Later work evaluating Cisco populations in Lake Superior (Hoff 2004; Stockwell et al. 2009; Rook et al. 2012; Myers et al. 2015) and

Bloater *C. hoyi* populations within Lakes Huron, Michigan, and Superior (Bunnell et al. 2010) observed large 10 to 2,795-fold differences in year-class strength as measured by densities of age-0 or age-1 fish. Yule et al. (2008) showed how age underestimation associated with scale-derived ages could lead to an inaccurate understanding of the regular production of strong year-classes of Lake Superior Cisco. Interannual variability in Kiyi year-class strength has not been evaluated.

The purpose of this study was to 1) compare Lake Superior Kiyi ages estimated from scales and otoliths, 2) evaluate variability in year-class strength, and 3) assess the validity of otolith-derived Kiyi ages by comparing the distribution of age estimates to strong year-classes identified from annual length frequency distributions.

Methods

Age analyses. –

Fish collections were made at 102 locations throughout Lake Superior (Figure 1) during daylight between 19 May and 20 July 2014. Collections were made with the U. S. Geological Survey Research Vessel Kiyi using a Yankee bottom trawl with either a chain or rubber disk foot rope towed at approximately 3.5 km/h. Both nets had an 11.9 m head rope, 15.5 m foot rope, and 2.2 m wing height with stretch meshes of 89 mm at the mouth, 64 mm for the trammel, and 13 mm at the cod-end. Nearshore trawling in May and June was cross-contour with a mean beginning depth of 19 m (range: 11-40), ending depth of 61 m (range: 19-144), and distance covered of 1.7 km (range: 0.5-3.8). Offshore trawling in July followed a constant depth contour with a mean average depth of 191 m (range: 92-315) and distance covered of 1.4 km (range: 1.2-1.5). Trawl distance was determined from the ship's geographic positioning system. Kiyi were identified based on morphological characteristics, such as fin length and eye diameter, as described in Koelz (1927) and Eshenroder et al. (2016). Individuals for which identification was ambiguous were not included in this study. All Kiyi collected were counted, weighed in aggregate, and frozen for later processing. Relative density (fish/ha) and biomass (kg/ha) were estimated by dividing collection counts and aggregate weights by the area swept by each trawl tow.

Frozen fish were thawed at room temperature before total length to the nearest mm, weight to the nearest gram, and sex (visually determined as female, male, or juvenile) were recorded. A

lakewide representative sample for estimating age was obtained by selecting 10 individuals per 10 mm length bin from fish ≥ 160 mm collected in each of five regions (Figure 1). All fish <160 mm were selected for estimating age because fish of this size were rare. Scales were removed from either side of the fish directly above the lateral line as close to the anterior margin of the dorsal fin as possible (Hogman 1968). Scales and sagittal otoliths were placed in paper envelopes to air dry.

Otoliths were embedded in clear epoxy (Buehler EpoKwick™ Epoxy, 5:1 ratio of resin to hardener) before a 0.5-mm thick section through the nucleus along the dorsoventral plane was obtained with a Buehler IsoMet™ Low Speed Saw. Otolith thin sections were lightly polished with 1000-grit sandpaper before viewing in mineral oil on a black background with reflected light applied at approximately a 45 degree angle to the section. A digital image of each thin section (Figure 2) was captured with a Nikon DS-Fi2™ camera attached to a Nikon SMZ745T™ stereo microscope. Multiple images were used for some otolith sections where a single image that was clear and focused in all areas could not be obtained. Age estimates were also obtained from scales for fish collected from the eastern Michigan region. Age was estimated from scales for a limited number of fish because a clear difference in age estimates between scales and otoliths was expected, as shown for numerous other fish including other coregonines (e.g., Maceina et al. 2007; Yule et al. 2008; Quist et al. 2012; Stewart et al. 2016). Digital images were captured from scales pressed into 5-mm thick acetate slides with the same camera and microscope described for otoliths.

Two readers, who were blind to any biological information related to the fish, identified annuli on otoliths from the digital images. The combination of a translucent band representing fast growth and an opaque band representing slow growth on the sectioned otolith was interpreted as one year of growth (Figure 2). Only completed opaque bands at the otolith margin were counted as an annulus, as partial growth from the capture year was present for some individuals. After initial analyses that compared age estimates between readers (see below), the two readers further reviewed the otolith image in an attempt to achieve a consensus age estimate for analyses that required a single estimate of age. Fish for which a consensus age estimate could not be achieved were removed from further analyses. One reader, who like the two otolith readers, was blind to biological information about the fish, identified annuli on scales using “cutting-over” and “compaction” characteristics evident in the circuli (Quist et al. 2012).

Bias in otolith-derived age estimates between two readers (e.g., one reader consistently estimated lower ages than the other reader) and between scale and otolith-derived age estimates from the same reader were assessed with modified age-bias plots (Campana et al. 1995; Muir et al. 2008) and the Evans and Hoenig (1995) test of symmetry for the age-agreement table (as suggested for use by McBride 2015). If no statistically significant bias between readers was detected for otolith-derived age estimates, then precision between readers was summarized as the percentage of fish for which the ages differed by zero or by one or fewer years and the average coefficient of variation (Chang 1982; Kimura and Lyons 1991). Age bias and precision metrics were computed with the `ageBias` and `agePrecision` functions, respectively, from the FSA package v0.8.12 (Ogle 2017) in the RTM statistical environment v3.3.3 (R Development Core Team 2017). All tests used $\alpha=0.05$ to determine statistical significance.

An age-length key (Fridriksson 1934; Ketchen 1949) was constructed from consensus otolith-derived age estimates. The age-length key was then used to assign specific ages to all Kiyi captured in 2014 using the method described by Isermann and Knight (2005) as implemented in the `alkIndivAge` function from the FSA package.

Length frequency year-class identification. –

Annual Kiyi length frequency data from the same locations and months and collected using the same methods were available from nearshore sites from 2003-2014 and from offshore sites from 2011-2014 (Vinson et al. 2016). Length frequency distributions from these years were visually examined for evidence of strong year-classes (i.e., recruitment) which could be used to assess the validity of the estimated ages for Kiyi captured in 2014. Kiyi likely hatch at a size (10-12 mm) and time (spring) similar to Cisco (Oyadomari and Auer 2007, 2008) and were likely not present as age-0 fish in these annual trawl samples. In Lake Michigan, Kiyi reached a mean standard length of approximately 100 mm the following spring at age-1 (Deason and Hile 1947). Thus, clusters of fish in our annual spring and summer collections with distinct modes less than 110 mm total length were identified as age-1 fish. The relative numbers of age-1 fish in these samples was used as an index for the strength of the previous year's year-class of Kiyi.

<A>Results

A total of 984 Kiyi were collected at 24 of the 102 locations sampled in 2014 (Figure 1). Kiyi were found at three nearshore locations between 27 May 2014 and 5 June 2014, and at 21 offshore locations between 7 July and 20 July 2014. Biomass and density estimates from individual trawl tows ranged from 0-12 kg/ha and 0-253 fish/ha, respectively. The minimum and maximum depths of capture at 21 on-contour sampling locations were 132 and 256 m. Maximum biomass (12 kg/ha) and density (253 fish/ha) were observed at 190 m. Kiyi total lengths ranged from 108-266 mm with a mean of 197 (SD, 19.3) mm.

Age analyses

Ages in 2014 were estimated from 288 thin-sectioned otoliths. Of these, 22 (7.6%) otoliths were deemed unreadable (cracked or cloudy image) and were removed from further consideration. There was no statistically significant systematic bias in otolith-derived age estimates between the two readers ($P = 0.445$; Figure 3), though the mean estimated age for the second reader was slightly greater when the first reader estimated an age of 5 (95% CI: 5.1-5.4; $P < 0.001$) and slightly lower when the first reader estimated an age of 12 (95% CI: 11.1-11.8; $P = 0.031$). Otolith-derived age estimates from the two readers agreed perfectly for 72.6% of the fish, agreed within one year for 97.0% of the fish, and had an average coefficient of variation of 2.8. Mean scale-derived age estimates were less than the otolith-derived age estimate for the same fish ($P < 0.039$), except for age-4 (Figure 4).

The maximum estimated age was 20 for females and 12 for males from otoliths and 8 for females and 7 for males from scales. The minimum estimated age was 4 from both otoliths and scales. The distribution of otolith-derived age estimates for Kiyi captured in 2014 showed distinct modes at age 11 and ages 5 or 6 (Figure 5), which correspond to the 2003, 2008, and 2009 year-classes.

Length frequency year-class identification

Examination of Kiyi length frequency distributions from fish captured in 2003-2014 showed that clusters of fish with a mode < 110 mm were present in high numbers in 2004, 2006, and 2010 and were not detected or at very low numbers in all other years (Figure 6). The fish in these clusters correspond to the 2003, 2005 and 2009 year-classes, respectively. The cluster of Kiyi in the 2003 year-class was distinct in subsequent years until at least 2006. In 2007, the cluster of

Kiyi from the 2005 year-class were either not evident or had grown enough to be indistinguishable from Kiyi of the 2003 year-class. Kiyi from the 2009 year-class were still distinct in 2010 but were either not evident or had grown enough to be indistinguishable from older fish by 2013. Only one distinct mode was evident in the length frequency distribution from 2014.

<A>Discussion

Precision between readers for thin-sectioned otoliths was very good as the average coefficient of variation (2.8) was less than 5, which Campana (2001) suggested represented “high precision.” This result was somewhat surprising because both readers expressed difficulty interpreting putative annuli near the center of otoliths when few annuli were present (i.e., relatively young fish) and at the margin on all otoliths (Figure 2). Due to the sporadic production of year-classes, no fish with an otolith-derived age less than four were collected in 2014. Without these young fish, an understanding of the appearance of the first few annuli could not be developed. Interpretation of the otolith margin is notoriously difficult (Campana 2001) and a better understanding of the otolith margin also could not be developed because our samples were restricted to two days in early June and a few days in mid-July, rather than throughout the May to September growing season. However, length frequency distributions for three other years when Kiyi were sampled in several months suggested that substantial growth in length of Lake Superior Kiyi was not evident until at least late July. This suggests that little current season’s growth should have been observed on the otolith thin sections in our sample. However, 21% and 36% of the otoliths were categorized by reader 1 and reader 2, respectively, as having evidence for growth in the current season.

Kiyi ages estimated from otoliths were consistently greater than ages estimated from scales. This is consistent with previous results for Lake Superior Cisco (Yule et al. 2008) and Pygmy Whitefish *Prosopium coulteri* (Stewart et al. 2016), Canadian Lake Whitefish *Coregonus clupeaformis* (Mills and Beamish 1980; Barnes and Power 1984) and Round Whitefish *Prosopium cylindraceum* (Jessop 1972), European Vendace *Coregonus albula* (Aass 1972), as well as for many other fish (Maceina et al. 2007; Quist et al. 2012). Our maximum otolith-derived age estimates of 20 for females and 12 for males is similar to Pratt and Chong (2012) who observed maximum otolith-derived age estimates of 22 for females and 16 for males from

Kiyi collected in Canadian waters of Lake Superior and Gorman (2012) who reported Lake Superior Kiyi life spans as >20 years. These ages are similar to the maximum otolith-derived age estimates for Lake Superior Cisco (21 for female and 17 for male; Yule et al. 2008).

Distinct modes in length frequency distributions from 2003-2014 provided evidence for strong year classes and partially validate our otolith-derived age estimates. The mode of age-11 fish in 2014 corresponds well with the 2003 year-class and the mode of age-5 and 6 fish in 2014 corresponds, with some ageing error (see below), to the 2009 year-class present in the length frequency distributions. However, a mode of age-9 fish that would correspond to the 2005 year-class present in the length frequency distributions was not observed in 2014. This lack of age-9 fish in our 2014 age analysis could be attributed to the apparent smaller size of that year-class as compared to the 2003 and 2009 year-classes. Thus, with the exception of age-9 fish, our otolith-derived age estimates from 2014 were generally within one year of ages corresponding to strong year-classes of Kiyi.

From these findings, it appears Kiyi age may be reliably estimated to within one year by examination of thin-sectioned otoliths. Ageing error may be reduced with a better understanding of the characteristics of the first few annuli and the appearance of the otolith margin. It is recommended that otoliths be collected from small (young) Kiyi in years when they are present and from Kiyi collected throughout the open-water growing season when feasible. Continued annual collections of length frequency data, along with otoliths from these fish, will allow for further validation of Kiyi age estimates from otoliths. Because otoliths appear to provide an accurate estimate of age, and age estimates from scales were less than that from otoliths for all otolith-derived ages, scales should no longer be used to estimate the age of Kiyi.

The annual length frequency distributions suggest that Kiyi experience high interannual variability in year-class strength. Only three strong year-classes were observed at age-1 from 2003-2014. Variable recruitment has been observed in other *Coregonus* spp. (e.g., *C. albula*, Axenrot & Degerman 2015; *C. artedi*, Hoff 2004; Stockwell et al. 2009; Myers et al. 2015; *C. autumnalis*, Fechhelm and Fissel 1988; Fechhelm and Griffiths 1990; *C. hoyi*, Bunnell et al. 2006, 2010; Gorman 2012; Collingsworth et al. 2014; and *C. zenithicus*, Gorman 2012). Strong Kiyi year-classes in 2003, 2005, and 2009 correspond to higher than average year-class strengths of Lake Superior Bloater and Cisco (Stockwell et al. 2009; Yule et al. 2008; more recent data in Vinson et al. 2016). Recruitment synchrony has also been observed within Bloater (Bunnell et

al., 2006, 2010) and Cisco (Myers et al. 2015) populations across the Great Lakes and in Europe (Sandström et al. 2014). Hypothesized factors underlying *Coregonus* spp. year-class strength variation includes density-independent physical environmental factors such as annual weather patterns that affect larval fishes directly or their food (Axenrot and Degerman 2015), density-dependent biotic factors (e.g., predation by or competition with Rainbow Smelt; Myers et al. 2015) or spawner sex ratios (Bunnell et al. 2006), or a combination of these factors. Synchrony among disjunct populations and between species in the same region supports the idea that environmental factors such as winter ice conditions, spring ice break-up date, and wind play a major role in determining year-class strength of *Coregonus* spp.

Our results indicate that Lake Superior Kiyi are long-lived and exhibit high inter-annual variability in year-class strength that may be synchronous with recruitment patterns exhibited by other *Coregonus* spp. The critical period for survival (*sensu* Hjort 1914; Houde 2008) appears to be prior to age-1 as distinct year-classes observed at age-1 appeared to survive to older ages. While currently not commercially or recreationally valuable like some *Coregonus* spp., Kiyi are a key trophic link between zooplankton and Lake Trout *Salvelinus namaycush*, the top native predator in the Great Lakes (Gamble et al. 2011), which is a commercially and recreationally important species. Successful restoration of deepwater ciscoes in the other Great Lakes may depend on understanding their life histories (Zimmerman and Krueger 2009). Additionally, Lake Superior is a refuge for many cold stenothermic species like Kiyi, which is currently listed as vulnerable on Canada's Endangered Species List (Turgeon and Bernatchez 2003). Increased study of and long-term monitoring of Kiyi and other cisco species, including age, growth, diet, and recruitment characteristics, may provide insight into how climate change may affect the deepwater fish fauna of Lake Superior and elsewhere.

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279 American Fisheries Society guidelines for the care and use of fishes
280 (<http://fisheries.org/docs/wp/Guidelines-for-Use-of-Fishes.pdf>).

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282 <A>References

- 283 Aass, P. 1972. Age determination and year-class fluctuation of Cisco, *Coregonus albula* L., in
284 the Mjøsa hydroelectric reservoir. Reports of the Institute of Freshwater Research
285 Drottningholm 52:5-22.
- 286 Axenrot, T., and E. Degerman. 2015. Year-class strength, physical fitness and recruitment cycles
287 in Vendace (*Coregonus albula*). Fisheries Research 173:61-69.
- 288 Barnes, M. A., and G. Power. 1984. A comparison of otolith and scale ages for western Labrador
289 Lake Whitefish, *Coregonus chupeaformis*. Environmental Biology of Fishes 10:297-299.
- 290 Beamish, R. J., and G. A. McFarlane. 1983. The forgotten requirement for age validation in
291 fisheries biology. Transactions of the American Fisheries Society 112:735-743.
- 292 Bunnell, D. B., C. P. Madenjian, and T. E. Croley II. 2006. Long-term trends of Bloater
293 (*Coregonus hoyi*) recruitment in Lake Michigan: evidence for the effect of sex ratio.
294 Canadian Journal of Fisheries and Aquatic Sciences 63:832-844.
- 295 Bunnell, D. B., J. V. Adams, O. T. Gorman, C. P. Madenjian, S. C. Riley, E. F. Roseman, and J.
296 S. Schaeffer. 2010. Population synchrony of a native fish across three Laurentian Great
297 Lakes: evaluating the effects of dispersal and climate. Oecologia 162:641-651.
- 298 Campana, S. E., M. C. Annand, and J. I. McMillan. 1995. Graphical and statistical methods for
299 determining the consistency of age determinations. Transactions of the American Fisheries
300 Society 124:131-138.
- 301 Campana, S. E. 2001. Accuracy, precision and quality control in age determination, including a
302 review of the use and abuse of age validation methods. Journal of Fish Biology 59:197-242.
- 303 Chang, W. Y. B. 1982. A statistical method for evaluating the reproducibility of age
304 determination. Canadian Journal of Fisheries and Aquatic Sciences 39:1208-1210.
- 305 Christie, W. J. 1974. Changes in the fish species composition of the Great Lakes. Journal of
306 Fisheries Research Board of Canada 31:827-854.
- 307 Collingsworth, P. D., D. B. Bunnell, C. P. Madenjian, and S. C. Riley. 2014. Comparative
308 recruitment dynamics of Alewife and Bloater in Lakes Michigan and Huron. Transactions of
309 the American Fisheries Society 143:294-309.

- 310 Deason, H. J., and R. Hile. 1947. Age and growth of the Kiyi, *Leucichthys kiyi* Koelz, in Lake
311 Michigan. Transactions of the American Fisheries Society 74:553-572.
- 312 Dryer, W. R., and J. Beil. 1964. Life history of Lake Herring in Lake Superior. Fishery Bulletin
313 63:493-530.
- 314 Eshenroder, R. L., P. Vecsei, O. T. Gorman, D. L. Yule, T. C. Pratt, N. E. Mandrak, D. B.
315 Bunnell, and A. M. Muir. 2016. Ciscoes (*Coregonus*, subgenus *Leucichthys*) of the
316 Laurentian Great Lakes and Lake Nipigon. Great Lakes Fishery Commission, Miscellaneous
317 Publication 2016-01. Available:
318 [http://www.glfc.org/pubs/misc/Ciscoes_of_the_Laurentian_Great_Lakes_and_Lake_Nipigon](http://www.glfc.org/pubs/misc/Ciscoes_of_the_Laurentian_Great_Lakes_and_Lake_Nipigon.pdf)
319 [.pdf](http://www.glfc.org/pubs/misc/Ciscoes_of_the_Laurentian_Great_Lakes_and_Lake_Nipigon.pdf) (January 2017)
- 320 Evans, G. T., and J. M. Hoenig. 1995. Analysing differences between two age determination
321 methods by tests of symmetry. Canadian Journal of Fisheries and Aquatic Sciences 52:364-
322 368.
- 323 Fechhelm, R. G., and D. B. Fissel. 1988. Wind-aided recruitment of Canadian Arctic Cisco
324 (*Coregonus autumnalis*) into Alaskan waters. Canadian Journal of Fisheries and Aquatic
325 Sciences 45:906-910.
- 326 Fechhelm, R. G., and W. B. Griffiths. 1990. Effect of wind on the recruitment of Canadian
327 Arctic Cisco (*Coregonus autumnalis*) into the central Alaskan Beaufort Sea. Canadian
328 Journal of Fisheries and Aquatic Sciences 47:2164-2171.
- 329 Fridriksson, A. 1934. On the calculation of age-distribution within a stock of Cod by means of
330 relatively few age-determinations as a key to measurements on a large scale. Rapports et
331 Proces-verbaux des Réunions. Conseil International pour l'Exploration de la Mer 86:1-5.
- 332 Gamble, A. E., T. R. Hrabik, J. D. Stockwell, and D. L. Yule. 2011. Trophic connections in Lake
333 Superior Part I: the offshore fish community. Journal of Great Lakes Research 37:541-549.
- 334 Gorman, O. T. 2012. Successional change in the Lake Superior fish community: population
335 trends in Ciscoes, Rainbow Smelt, and Lake Trout, 1958-2008. Advances in Limnology
336 63:337-362.
- 337 Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of
338 biological research. Rapports et Proces-verbaux des Réunions. Conseil International pour
339 l'Exploration de la Mer 20:1-228.

- Hoff, M. H. 2004. Biotic and abiotic factors related to Lake Herring recruitment in the Wisconsin waters of Lake Superior, 1984–1998. *Journal of Great Lakes Research* 30:423-433.
- Hogman, W. J. 1968. Annulus formation on scales of four species of coregonids reared under artificial conditions. *Journal of the Fisheries Research Board of Canada* 25:2111-2122.
- Houde, E. D. 2008. Emerging from Hjort's shadow. *Journal of Northwest Atlantic Fishery Science* 41:53-70.
- Isermann, D. A., and C. T. Knight. 2005. A computer program for age–length keys incorporating age assignment to individual fish. *North American Journal of Fisheries Management*, 25:1153-1160.
- Jessop, B. M. 1972. Aging Round Whitefish (*Prosopium cylindraceum*) of the Leaf River, Ungava, Quebec, by otoliths. *Journal of the Fisheries Research Board of Canada* 29:452-454.
- Ketchen, K. S. 1949. Stratified subsampling for determining age distributions. *Transactions of the American Fisheries Society* 79:205-212.
- Kimura, D. K., and J. J. Lyons. 1991. Between reader bias and variability in age-determination process. *Fishery Bulletin* 89:53-60.
- Koelz, W. N. 1927. Coregonid fishes of the Great Lakes. United States Bureau of Fisheries 43:297-643.
- Maceina, M. J., J. Boxrucker, D. L. Bueckmeier, R. S. Gangl, D. O. Lucchesi, D. A. Isermann, J. R. Jackson, and P. J. Martinez. 2007. Current status and review of freshwater fish aging procedures used by state and provincial fisheries agencies with recommendations for future directions. *Fisheries* 32:329-340.
- McBride, R. S. 2015. Diagnosis of paired age agreement: a simulation approach of accuracy and precision effects. *ICES Journal of Marine Science* 72:2149-2167.
- Mills, K. H., and R. J. Beamish. 1980. Comparison of fin-ray and scale age determinations for Lake Whitefish (*Coregonus clupeaformis*) and their implications for estimates of growth and annual survival. *Canadian Journal of Fisheries and Aquatic Sciences* 37:534–544.
- Moffett, J. W. 1957. Recent changes in the deep-water fish populations of Lake Michigan. *Transactions of the American Fisheries Society* 86:393-408.

- 369 Muir, A. M., M. P. Ebener, J. X. He, and J. E. Johnson. 2008. A comparison of the scale and
370 otolith methods of age estimation for Lake Whitefish in Lake Huron. North American
371 Journal of Fisheries Management 28:625-635.
- 372 Myers, J. T., D. L. Yule, M. I. Jones, T. D. Ahrenstorff, T. R. Hrabik, R. M. Claramunt, M. P.
373 Ebener, and E. K. Berglund. 2015. Spatial synchrony in Cisco recruitment. Fishery Research
374 165:11-21.
- 375 Ogle, D. H. 2017. FSA: Fisheries stock analysis. Available: <http://github.com/droglenc/fsa/>.
- 376 Oyadomari, J. K., and N. A. Auer. 2007. Influence of rearing temperature and feeding regime on
377 otolith increment deposition of larval Ciscos. Transactions of the American Fisheries
378 Society 136:766-777.
- 379 Oyadomari, J. K., and N. A. Auer. 2008. Transport and growth of larval Cisco (*Coregonus*
380 *artedi*) in the Keweenaw Current region of Lake Superior. Canadian Journal of Fisheries and
381 Aquatic Sciences 65:1447-1458.
- 382 Parker, B. J. 1989. Status of the Kiyi, *Coregonus kiyi*, in Canada. Canadian Field-Naturalist
383 103:171-174.
- 384 Pratt, T. C., and S. C. Chong. 2012. Contemporary life history characteristics of Lake Superior
385 deepwater ciscos. Aquatic Ecosystem Health and Management 15:322-332.
- 386 Quist, M. C., M. A. Pegg, and D. R. DeVries. 2012. Age and growth. Pages 677-731 in A. V.
387 Zale, D. L. Parrish, and T. M. Sutton, editors. Fisheries Techniques, 3rd edition. American
388 Fisheries Society, Bethesda, Maryland.
- 389 R Development Core Team. 2017. R: a language and environment for statistical computing. R
390 Foundation for Statistical Computing. Available: <http://R-project.org>.
- 391 Rook, B. J., M. J. Hansen, and O. T. Gorman, 2012. The spatial scale for cisco recruitment
392 dynamics in Lake Superior during 1978–2007. North American Journal of Fisheries
393 Management 32:499-514.
- 394 Sandström, A., H. Ragnarsson-Stabo, T. Axenrot, and E. Bergstrand. 2014. Has climate
395 variability driven the trends and dynamics in recruitment of pelagic fish species in Swedish
396 Lakes Vänern and Vättern in recent decades? Aquatic Ecosystem Health and Management
397 17:349-356.

- Smith, S. H. 1964. Status of the deepwater cisco population of Lake Michigan. Transactions of the American Fisheries Society 93:155-163.
- Stewart, T. R., D. H. Ogle, O. T. Gorman, and M. R. Vinson. 2016. Age, growth, and size of Lake Superior Pygmy Whitefish (*Prosopium coulterii*). The American Midland Naturalist Journal 175:24-36.
- Stockwell, J. D., M. P. Ebener, J. A. Black, O. T. Gorman, T. R. Hrabik, R. E. Kinnunen, W. P. Mattes, J. K. Oyadomari, S. T. Schram, D. R. Schreiner, M. J. Seider, S. P. Sitar, and D. L. Yule. 2009. A synthesis of Cisco recovery in Lake Superior: implications for native fish rehabilitation in the Laurentian Great Lakes. North American Journal of Fisheries Management 29:626-652.
- Turgeon, J., and L. Bernatchez. 2003. Reticulate evolution and phenotypic diversity in North American ciscoes, *Coregonus* ssp. (Teleostei: Salmonidae): implications for the conservation of an evolutionary legacy. Conservation Genetics 4:67-81.
- Vinson, M. R., L. M. Evrard, O. T. Gorman, and D. L. Yule. 2016. Compiled reports to the Great Lakes Fishery Commission of the annual bottom trawl and acoustics surveys, 2015, Ann Arbor, MI, pp. 86-96. Available: http://www.glfc.org/lakecom/common_docs/Compiled%20Reports%20from%20USGS%202016.pdf. (November 2016).
- Yule, D. L., J. D. Stockwell, J. A. Black, K. I. Cullis, G. A. Cholwek, and J. T. Myers. 2008. How systematic age underestimation can impede understanding of fish population dynamics: Lessons learned from a Lake Superior Cisco stock. Transactions of the American Fisheries Society 137:481-495.
- Yule, D. L., J. V. Adams, T. R. Hrabik, M. R. Vinson, Z. Woiak, and T. D. Ahrenstorff. 2013. Use of classification trees to apportion single echo detections to species: application to the pelagic fish community of Lake Superior. Fishery Research 140:123-132.
- Zimmerman, M. S., and C. C. Krueger. 2009. An ecosystem perspective on re-establishing native deepwater fishes in the Laurentian Great Lakes. North American Journal of Fisheries Management 29:1352-1371.

Figure Captions

Figure 1. Sampling locations in Lake Superior and the five regions used for subsampling Kiyi for age estimation in 2014. Squares denote offshore sites and circles denote nearshore sites. Solid symbols denote locations where Kiyi were collected in 2014.

Figure 2. Thin-sectioned otolith from a 206-mm male Kiyi captured at an offshore site in the northern Ontario region on 20-Jul-2014 that was estimated to be 11 years old. The length of the white bar is 1 mm.

Figure 3. Difference in otolith-derived age estimates for Lake Superior Kiyi between two readers by age estimates for the first reader. Darker points represent more individuals. The open diamonds and vertical lines at each age estimate for the first reader are the mean and 95% confidence intervals, respectively, for the difference in age estimates between readers. Confidence intervals that do not contain zero indicate a statistically significant difference in age estimates between readers. Sample sizes for each age estimate for the first reader are shown above the x-axis.

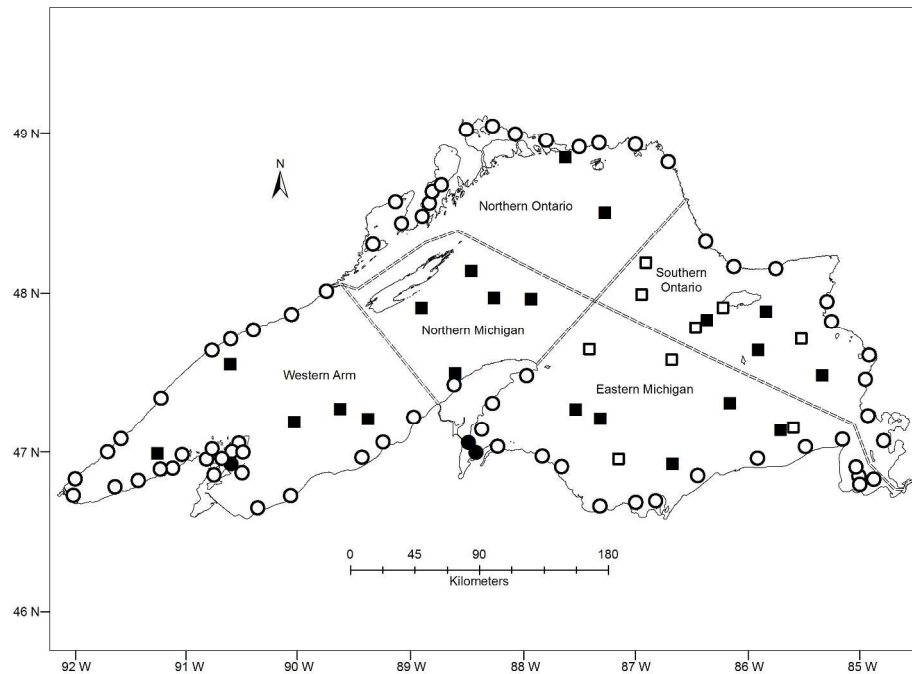
Figure 4. Difference in scale- and otolith-derived age estimates for Lake Superior Kiyi by otolith-derived age estimates. All fish were collected from only the eastern Michigan region. Darker points represent more individuals. The open diamonds and vertical lines at each otolith-derived age estimate are the mean and 95% confidence intervals, respectively, for the difference in scale- and otolith-derived age estimates. Confidence intervals that do not contain zero indicate a statistically significant difference in age estimates between scales and otoliths. Sample sizes for each otolith-derived age estimate are shown above the x-axis.

Figure 5. Frequency of otolith-derived age estimates for all Lake Superior Kiyi captured from May-July 2014. Ages were expanded from an age-length key based on consensus otolith-derived age estimates between two readers.

Figure 6. Relative within-year frequency of total length for all Lake Superior Kiyi captured in May-July from nearshore locations in 2003-2010 and both nearshore and offshore locations in 2011-2014. Plots are labeled with the year sampled and the total sample size. Each plot is scaled

458 such that the mode has a height equal to 1. Numeric labels in 2004, 2006, and 2010 are the age
459 fish in those modes were in 2014. The dashed vertical line in each plot at 110 mm was used to
460 identify the total length mode for age-1 fish.

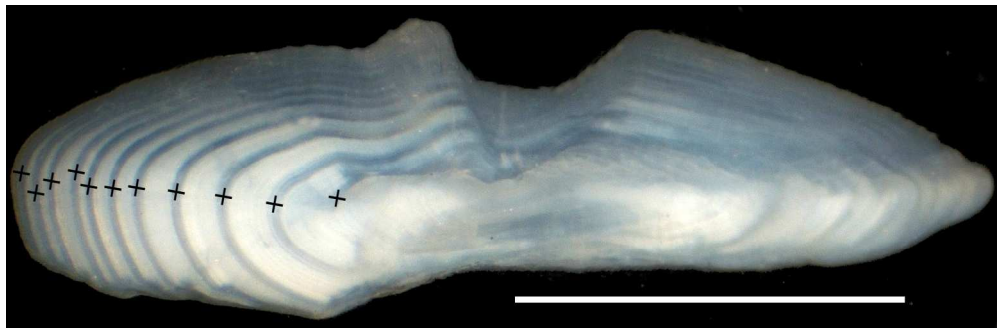
For Peer Review Only



Sampling locations in Lake Superior and the five regions used for subsampling Kiyi for age estimation in 2014. Squares denote offshore sites and circles denote nearshore sites. Solid symbols denote locations where Kiyi were collected in 2014.

Figure 1

1164x899mm (72 x 72 DPI)

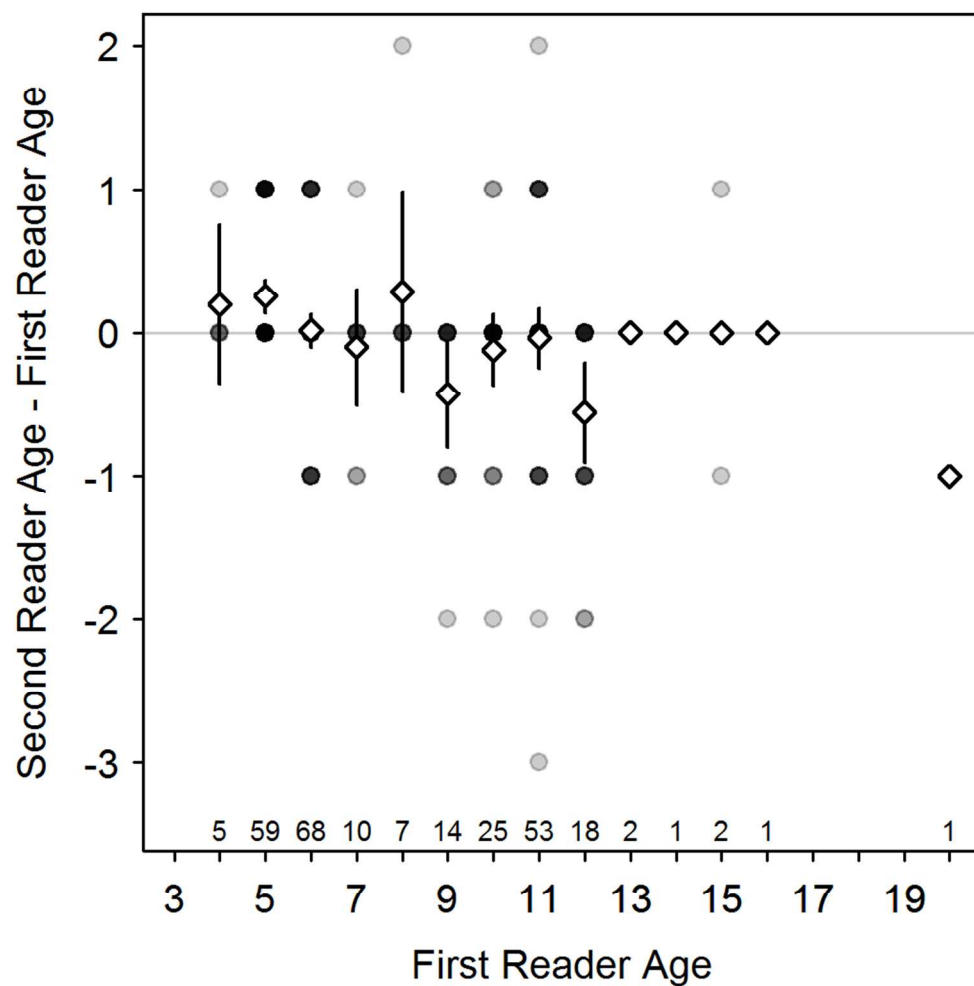


Thin-sectioned otolith from a 206-mm male Kiyi captured at an offshore site in the northern Ontario region on 20-Jul-2014 that was estimated to be 11 years old. The length of the white bar is 1 mm.

Figure 2

760x246mm (72 x 72 DPI)

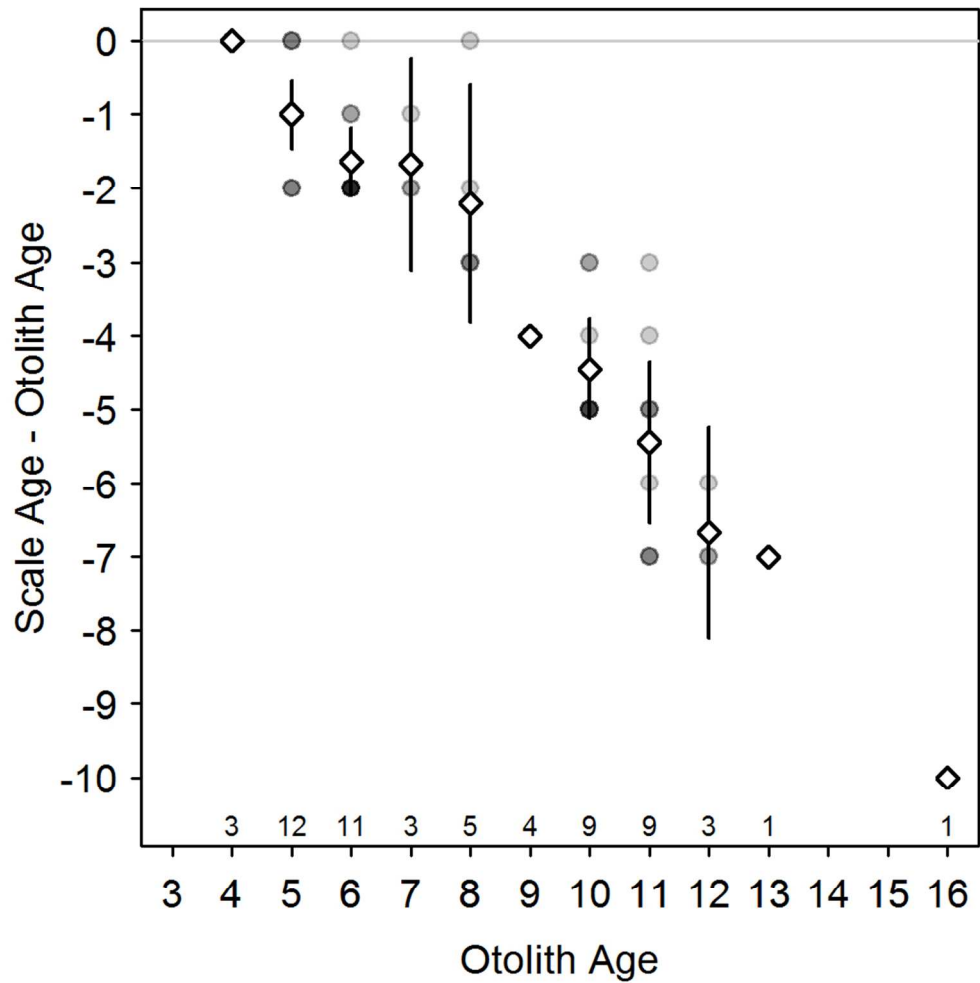
Peer Review Only



Difference in otolith-derived age estimates for Lake Superior Kiyi between two readers by age estimates for the first reader. Darker points represent more individuals. The open diamonds and vertical lines at each age estimate for the first reader are the mean and 95% confidence intervals, respectively, for the difference in age estimates between readers. Confidence intervals that do not contain zero indicate a statistically significant difference in age estimates between readers. Sample sizes for each age estimate for the first reader are shown above the x-axis.

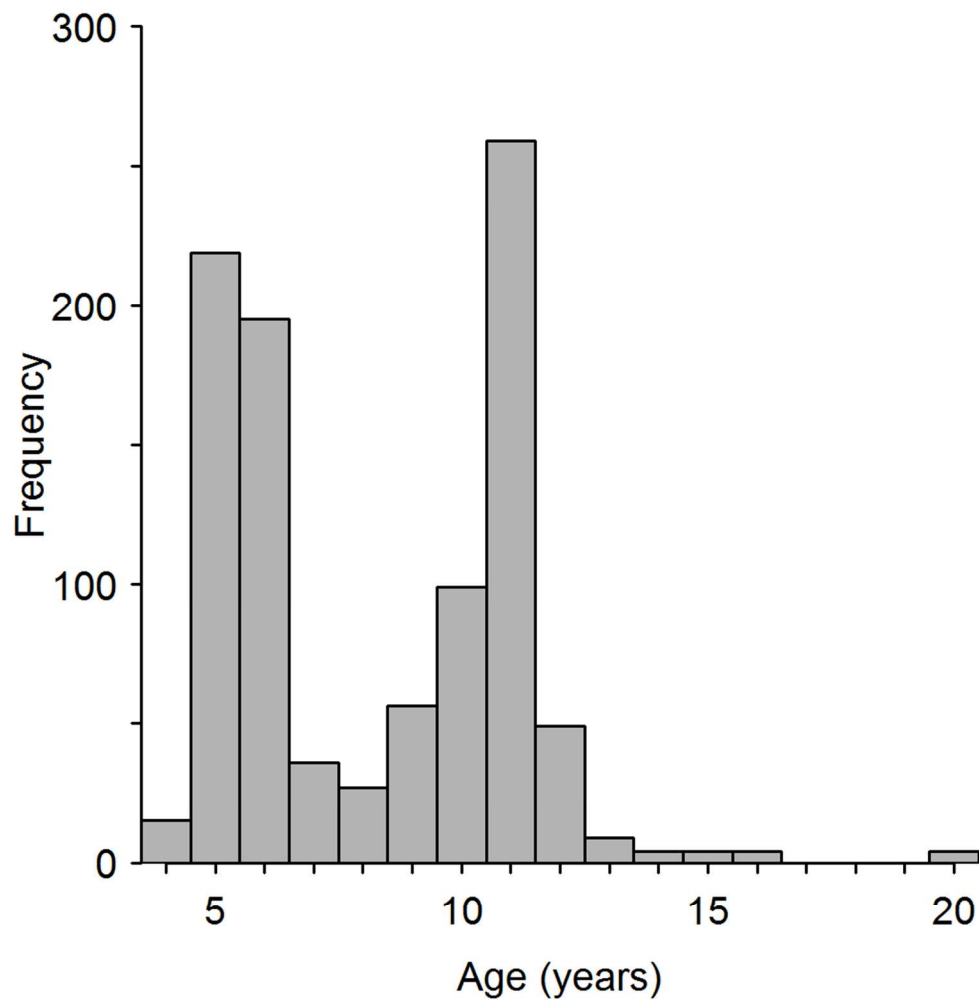
Figure 3

88x88mm (300 x 300 DPI)



Difference in scale- and otolith-derived age estimates for Lake Superior Kiyi by otolith-derived age estimates. All fish were collected from only the eastern Michigan region. Darker points represent more individuals. The open diamonds and vertical lines at each otolith-derived age estimate are the mean and 95% confidence intervals, respectively, for the difference in scale- and otolith-derived age estimates. Confidence intervals that do not contain zero indicate a statistically significant difference in age estimates between scales and otoliths. Sample sizes for each otolith-derived age estimate are shown above the x-axis.

Figure 4
88x88mm (300 x 300 DPI)

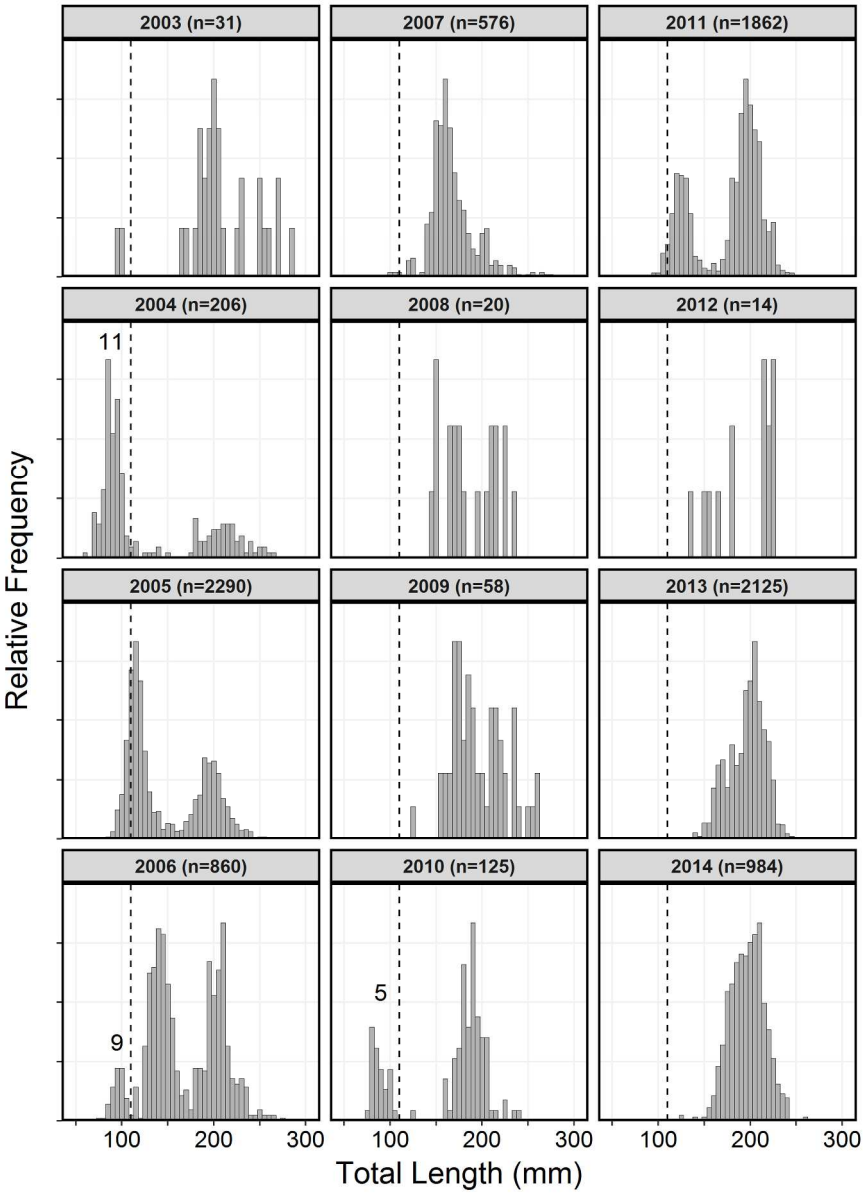


Frequency of otolith-derived age estimates for all Lake Superior Kiyi captured from May-July 2014. Ages were expanded from an age-length key based on consensus otolith-derived age estimates between two readers.

Figure 5

88x88mm (300 x 300 DPI)





Relative within-year frequency of total length for all Lake Superior Kiyi captured in May-July from nearshore locations in 2003-2010 and both nearshore and offshore locations in 2011-2014. Plots are labeled with the year sampled and the total sample size. Each plot is scaled such that the mode has a height equal to 1. Numeric labels in 2004, 2006, and 2010 are the age fish in those modes were in 2014. The dashed vertical line in each plot at 110 mm was used to identify the total length mode for age-1 fish.

Figure 6
184x254mm (300 x 300 DPI)